THE MORPHOLOGY AND LIFE–HISTORY OF *NEOPECHONA PYRIFORME* (LINTON, 1900) N. GEN., N. COMB. (TREMATODA: LEPOCREADIIDAE) [1]

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Linton (1900) described *Distomum pyriforme* n. sp., from the pyloric ceca and intestine of the rudderfish, *Palinurichthys perciformis,* taken at Woods Hole, Massachusetts, on four occasions in August, 1898. The description states, p. 292, "Body very slightly compressed, of various shapes, but usually elliptical or pyriform in outline, armed with low, flat, rounded, scale-like spines. Neck in some slightly extended; in others the oral sucker was retracted (Fig. 56)." The latter feature appears to be characteristic since Linton noted, p. 293, "A large portion of the preserved specimens have the anterior end of the body inverted." His Figure 57 was made from a longitudinal, frontal section showing the inverted anterior end of a worm with a tubular canal from the retracted oral sucker to the surface of the body. The species was illustrated with Figures 52–59. The type material consists of more than 100 specimens, mounted on eight slides, deposited in the Helminthological Collection of the U. S. National Museum under the number 6516. All of the worms are juvenile, with immature gonads and diffuse pigment, from disintegrating ocelli, in the lateral pharyngeal areas. The measurements of specimens were made on young, half-grown individuals and have little value. The account, however, contains much significant information, especially the report on living specimens, some of which were mature, since there are observations on the spinose cirrus, the relatively large seminal vesicle and prostate, voluminous vitellaria, and the size of eggs. Figures 55 and 56 are particularly interesting; they demonstrate the confused and inadequate status of the specific description. In Figure 55, the ceca terminate at the anterior border of the excretory vesicle, midway between the acetabulum and the posterior end of the body, while the excretory vesicle is represented as saccate, extending forward only to the caudal ends of the ceca. It is probable that the caudal portions of the ceca and the anterior extension of the excretory vesicle were not observed since in Figure 56, the same structures are represented very differently; the ceca extend to the posterior end of the body while the excretory vesicle extends forward to the level of the acetabulum and contains a row of concretions. The text, p. 292 states, "Intestinal branches conspicuous, straight, reaching the posterior end of the body." On p. 293 there is the statement, "Spherical bodies with a concentric structure were seen lying in the excretory vesicle. These masses were not of uniform size; the largest measured 0.010 mm in diameter. They appear to be solid excreta. They are much smaller than the ova and moreover are spherical." The description and figures, although confused and incomplete, are definite enough to identify the species and validate the specific name.

Linton (1901) reported *D. pyriforme* from five different species of fishes at Woods Hole: *Palinurichthys perciformis;* the squeteague, *Cynoscion regalis;* the kingfish, *Menticirrhus saxatilis;* the summer flounder, *Paralichthys dentatus;* and the scup, *Stenotomus chrysops.* Specimens from *S. chrysops* were described and illustrated, Figure 346. This figure is consistent with Figure 56 of his (1900) paper.

Linton (1905) recorded *D. pyriforme* from fishes taken at Beaufort, North Carolina, including the menhaden, *Brevoortia tyrannus;* the pinfish, *Lagodon rhomboides;* and the silversides, *Menidia menidia.* There were no descriptions or figures.

Linton (1940) transferred *D. pyriforme* to the genus *Lepocreadium* Stossich, 1904 as *L. pyriforme* (Linton). He stated, p. 84, "To this species are referred certain small distomes which, although differing in many details of structure, resemble each other sufficiently to warrant their inclusion in the same specific grouping when allowance is made for such differences as may be accounted for by varying conditions of contraction and age." The specific diagnosis is so indefinite and general that it might include a group of genera. The specimens, with dates of collection and brief descriptions, were reported from the sand-launce, *Ammodytes americanus;* the harvestfish, *Peprilus paru;* the cutlassfish, *Trichiurus lepturus;* the bluefish, *Pomatomus saltatrix;* and the dollarfish, *Poronotus triacanthus;* in addition to the other species listed earlier, *viz., P. perciformis, C. regalis, M. saxatilis; P. dentatus;* and *S. chrysops. Lepocreadium pyriforme* was depicted by three figures; Figure 47 represents a specimen from *P. perciformis;* the source of Figure 48 is not given; and Figure 49 is of a worm from *P. triacanthus.* The specimens shown in Figures 47 and 49 are probably congeneric but obviously belong to different species. They differ in morphological detail, including relative length of prepharynx and esophagus and of the digestive ceca, and in extent of vitellaria. Linton did not designate a type of *Lepocreadium pyriforme.* Sogandares-Bernal and Hutton (1959) declared, p. 58, "Linton (1940) apparently has a heterogeneous assemblage of species listed under *Lepocreadium pyriforme.* Linton's (1940: Fig. 48) shows prostate cells surrounding the posterior end of the cirrus sac and it well may be that he confused a species of *Opechona* with *Lepocreadium.* Linton (1940) does not mention the presence of an epithelial esophagus. Here again a study of Linton's material is necessary." Sogandares-Bernal and Hutton (1960) discussed the status of some marine species of *Lepocreadium* Stossich, 1904 from the North American Atlantic and examined certain specimens from the Linton collection. The type material was not observed but specimens were depicted from *P. perciformis* (Figure 9), from *A. americanus* (Figure 10), and *Peprilus alepidotus* (Figure 12). They stated, p. 282, "The specimens pictured in figures 10 to 11 differ from the specimen pictured in Figure 9 by possessing a longer post-testicular space and vitellaria extending to cecal bifurcation and shorter prepharynx. The specimen pictured in Figure 12 differs from the specimens pictured in Figures 10 and 11 by possessing a cirrus sac which scarcely extends posterior to the acetabulum as compared with cirrus sac extending posterior to acetabulum by half the cirrus sac length, and from the specimen pictured in Figure 9 by possessing vitellaria which extend to the cecal bifurcation, shorter prepharynx and esophagus almost lacking. *L. pyriforme* should be redescribed if the holotype becomes available. The specimens studied here were not numerous enough to evaluate variation of the species. Figure

9 is identical with Linton's (1940) Figure 47 from the same host. There is little doubt that our Figure 9 and Linton's Figure 47 were drawn from the same specimens collected from the type host, *Palinurichthys perciformis.*" Nahhas and Cable (1964) listed a single, juvenile specimen from *P. paru* as *Lepocreadium pyriforme* (Linton, 1900) Linton, 1940, because of its similarity to his (1940) Figure 47. Nahhas and Short (1965) described *Lepocreadium brevoortia* n. sp., from the menhaden, *B. tyrannus,* and distinguished it from all 21 other species in the genus by the massive pharynx and spined cirrus. They stated, p. 43, "*L. pyriforme* (Linton, 1900) Linton, 1940 has a spiny cirrus. Sogandares-Bernal and Hutton (1960) discussed this species and concluded that there are several species involved in Linton's descriptions. Nahhas and Cable (1964) accepted as this species only individuals that are similar to Figure 47 (Linton, 1940) or Figure 9 (Sogandares-Bernal and Hutton, 1960)."

But the status of *Lepocreadium pyriforme* (Linton, 1900) Linton, 1940 remains anomalous. The specimens described and named *Distomum pyriforme* by Linton (1900) are not congeneric with those portrayed in his (1940) Figures 47 and 49 as representative of *Lepocreadium pyriforme.* Many species with divergent morphology have been assigned to *Lepocreadium* and as a result the generic concept has become indefinite and uncertain. Indeed, the genus *Lepocreadium* Stossich, 1904 is not clearly delimited. It was based on *Distomum album* Stossich (1890) from *Cantharus orbicularis* taken at Trieste. This species was included in the genus *Creadium* Looss, 1894 by Looss (1894). But *Creadium* was preoccupied as a generic name and was replaced by *Allocreadium* Looss, 1900. Stossich (1901) described *Allocreadium pegorchis* from *Maena smaris,* taken at Trieste, and he (1904) named the species, *album,* type of a new genus, *Lepocreadium,* in which he included *Lepocreadium pegorchis* (Stossich, 1901), transferred from *Allocreadium.* As diagnostic features of the new genus, Stossich listed: body elongate, cylindrical, rounded posteriorly, attenuated anteriorly; acetabulum at end of the anterior third of body, somewhat smaller than the terminal oral sucker. Digestive tract with prepharynx, robust and elongate pharynx, short esophagus, bifurcation immediately anterior to the acetabulum, ceca extend to posterior end of body. The figure in his (1890) report shows the ceca ending blindly. The testes are subspherical, contiguous, one immediately in front of the other; cirrus sac clavate, with seminal vesicle and spined cirrus. The genital pore is preacetabular, on left side, and the ovary globular, pretesticular, displaced to right of median plane. The vitellaria are well developed, and composed of numerous follicles which extend posteriorly from the level of the acetabulum to the posterior end of the body and become confluent posterior to the testes, and the uterus is short, between ovary and acetabulum; eggs few, large. The species is common in the pyloric ceca and anterior part of the intestine of *Cantharus orbicularis* and *Oblata melanura.*

The life-cycle and developmental stages of the species described as *Distomum pyriforme* Linton, 1900 are described in the present paper. The specimens differ from *Lepocreadium album* in many respects; the bifurcation of the digestive tract is nearer the anterior end; the ceca open into the posterior end of the excretory vesicle; the testes are diagonal, the left testis anterior to the right one; the vitellaria extend from the level of the pharynx to the posterior end of the body, but are not confluent in the median plane. These differences appear of generic significance and,

accordingly, *D. pyriforme* Linton, 1900 can not be included in the genus *Lepocreadium*.

The present investigation is an outgrowth of a survey of snails in the Woods Hole area, begun in an attempt to find the cercarial stages of two species of digenetic trematodes whose encysted metacercariae occur in the gills of *Fundulus heteroclitus* and *Fundulus majalis*. Examination of *Anachis avara* yielded an ophthalmotrichocercous cercaria whose body structure recalled the metacercaria from *Pleurobrachis pileus* which the writer had studied at Roscoff, France, thirty-five years before. The morphological agreement was striking. The larvae from *P. pileus*, known as *Opechona bacillaris* (Molin, 1859) have been observed repeatedly in Europe, but the life-cycle has not yet been elucidated. The species was described initially as *Distomum bacillare* by Molin (1859) on specimens from the intestine of *Centrophus pompilius* taken in the Adriatic. It was described by Olsson (1868) as *Distomum increscens* from *Scomber scombrus, Merluccius vulgaris*, and *Hippoglossus maximus* taken on the west coast of Sweden. Stossich (1887) redescribed *D. bacillare* (Molin, 1859) from *S. scombrus* taken at Trieste, but the account was imperfect and omitted certain important features. Odhner (1905) compared specimens of *D. bacillare* from the Adriatic with *D. increscens* Olsson and announced their identity. Lebour (1908) described specimens from the whiting, *Gadus merlangus*, taken off the Northumberland coast of England, as a new species, *Pharyngora retractilis*. The worms were similar to *D. bacillare*, but appeared to be distinct. Nicoll (1910) examined certain of Stossich's specimens of *D. bacillare* and recognized them as identical with *P. retractilis*, which he had found a common parasite of *S. scombrus* and *G. merlangus* in British waters. He redescribed the species as *Pharyngora bacillaris* (Molin, 1859). In the same paper, Nicoll (1910) reported a larval trematode, found in plankton tow, which agreed so completely with juvenile specimens of *P. bacillaris* found in fishes, that he was "practically certain" of their identity. Lebour (1916) reported unencysted metacercariae of *P. bacillaris* in the medusae of *Obelia* sp., *Cosmetira pilosella, Turris pileata* and *Phialidium hemisphericum* and in the ctenophore, *Pleurobrachia pileus*, taken at Plymouth. She (1917) recorded the metacercariae from *Sagitta bipunctata;* also, she described and figured an ophthalmotrichocercous cercaria, taken in tow netting, as the larva of *P. bacillaris*. Ward and Fillingham (1934) described *Opechona alaskenisis* from an unidentified toadfish, taken in Alaska. They recalled that Looss (1907) had designated *D. bacillare* (Molin, 1859) as type of a new genus, *Opechona*, that the publication by Looss was about one year earlier than the paper by Lebour in which she erected the genus *Pharyngora*, and since both generic names are based on *D. bacillare* Molin, 1859, *Opechona* has priority and *Pharyngora* disappears as a synonym.

THE LIFE-CYCLE

It has long been known that certain hydrozoan and scyphozoan medusae of the Woods Hole region harbor unencysted metacercariae of digenetic trematodes. The identity of these larval forms has never been established. In an abstract, Stunkard (1967a) reported natural infections in *Bougainvillia carolinensis, Gonionemus vertens*, and *Chrysaora quinquecirrha*. He also reported an undescribed ophthalmotrichocercous cercaria from *Anachis avara*, whose morphology closely paralleled that of the metacercariae in the jelly-fishes. To test the possibility of specific identity,
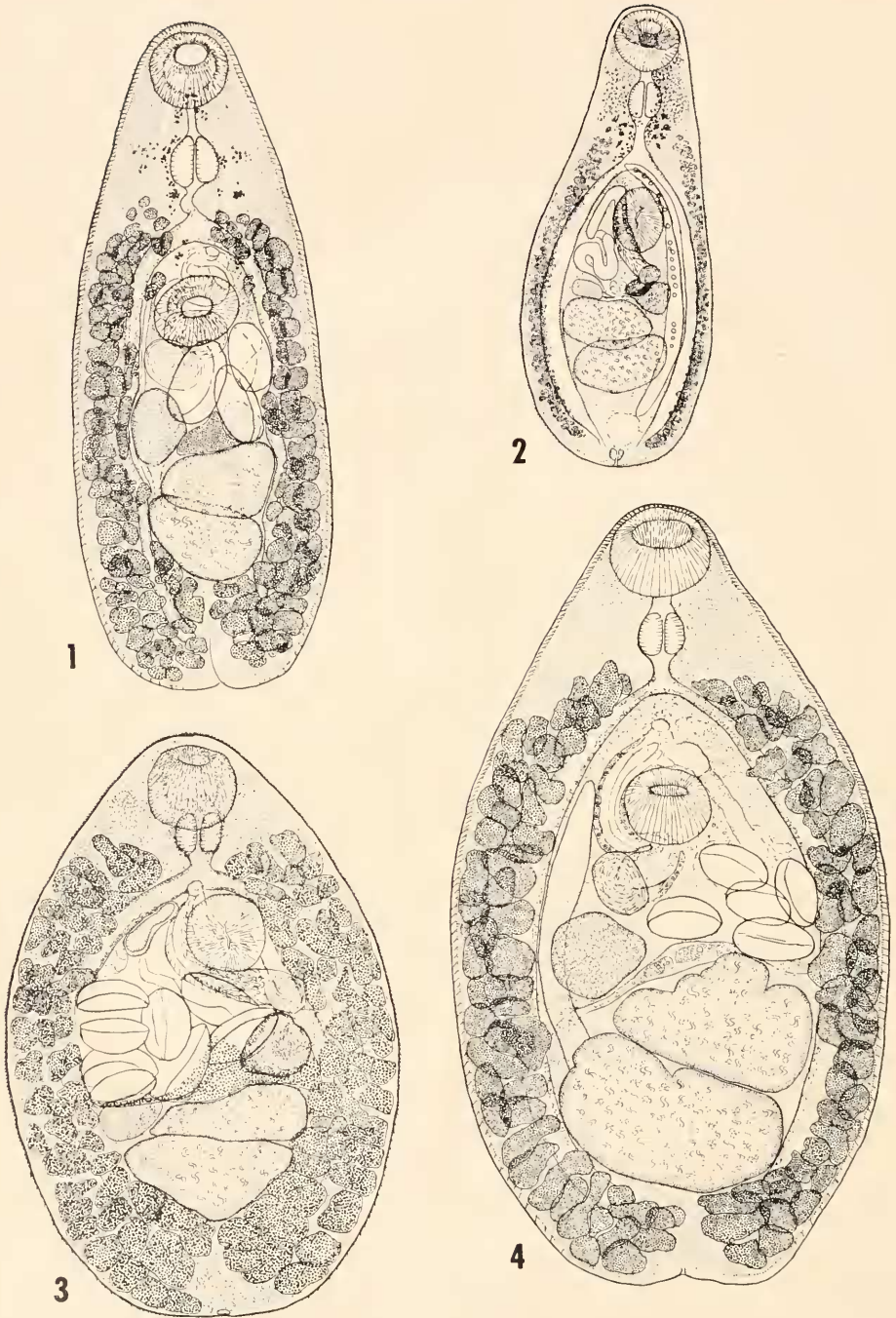
FIGURES 1-4.

individuals of *G. vertens* and *C. quinquecirrha* were exposed to these cercariae with resultant massive infections. The specimens of experimental infection were indistinguishable from those of natural infections. The metacercariae in medusae grow very slowly and very little; moreover, they are infective immediately, so the cnidarians are hardly more than paratenic hosts (hôtes d'attente). Early attempts to complete the life-cycle were unsuccessful, since fishes could be maintained for only brief periods in the small aquaria and warm water of the rooms in the Marine Biological Laboratory. Through the kindness of Mr. Charles L. Wheeler, Director of the Woods Hole Aquarium, large tanks with cold water were made available for infection experiments. Experimentally infected medusae, both *G. vertens* and *C. quinquecirrha,* were placed in aquaria with different species of fishes that had been in captivity for long periods. The scup, *S. chrysops,* and the sea-bass, *Centropristis striatus,* were the only species observed to eat the jellyfishes; other species: mackerel, *Scomber scombrus;* sea-robin, *Prionotus carolinus,* and the cunner, *Tautogolabrus adspersus;* apparently ignored the medusae. The fishes were fed four times at five day intervals. Only *S. chrysops* became infected. Four scup were exposed; a sea-bass ate one scup which was in the aquarium with it; the three remaining fishes, dissected four weeks after the first feeding, yielded 92 worms, ranging from juveniles to gravid specimens. One fish contained 47 worms, one 24 worms, and the third 20 worms. The juvenile specimens agree with the type specimens of *D. pyriforme* and the adult worms are so similar to the description and figures (Linton, 1900, Fig. 56; 1901, Fig. 346), that all must belong to a single species. The specimen portrayed in Linton's (1901) Figure 346 was taken from a scup. In the (1967a) report, Stunkard referred the worms to *Opechona* or a closely related genus, but final allocation was deferred pending information on the number and pattern of the flame-cells and penetration-glands of the cercaria.

The study of *D. pyriforme* was continued in the summer of 1968, which provided additional information and data on the excretory system and penetration-glands of the cercaria (Stunkard, 1968). Lebour (1916) reported unencysted metacercariae of *Pharyngora bacillaris* [=*Opechona bacillaris* (Molin, 1859) Looss, 1907] in various medusae and the ctenophore, *Pleurobrachia pileus,* and Stunkard (1932) found these larvae in the same ctenophore at Roscoff, on the Brittany coast of France. Martin (1945) reported unencysted metacercariae in the ctenophore, *Mnemiopsis leidyi,* at Woods Hole. These metacercariae were traced to trichocercous cercariae that developed in sporocysts and emerged from the bivalve mollusk, *Laevicardium mortoni.* Although the metacercariae were not closely related to *Opechona,* the presence of metacercariae in these ctenophores was an item of much interest. Accordingly in 1968, specimens of *M. leidyi* and of the scyphozoan, *Aurelia aurita,* were exposed to the cercariae from *A. avara.* The cercariae swarmed around the ctenophores, penetrated in enormous numbers, and

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FIGURE 1. Adult worm of *Neopechona,* natural infection, fixed without pressure, ventral view, length, 0.44 mm.
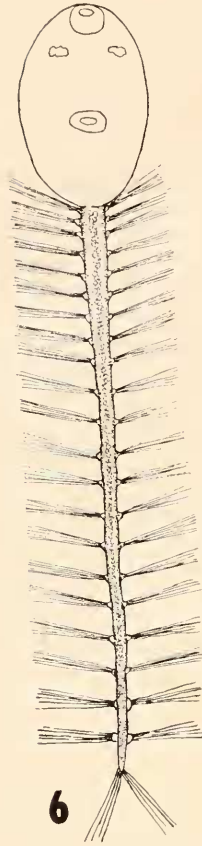
FIGURE 2. Juvenile specimen, experimental infection, fixed well extended, dorsal view, length 0.36 mm.

FIGURE 3. Adult worm, experimental infection, fixed under pressure, dorsal view, length, 0.50 mm.
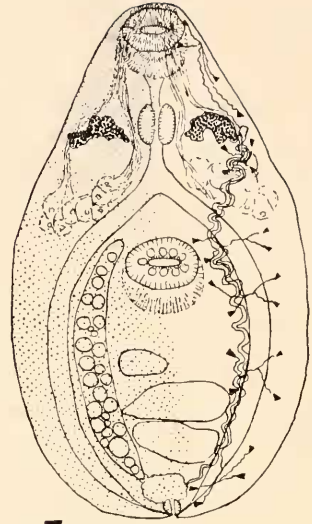
FIGURE 4. Adult worm, natural infection, fixed under pressure, ventral view, length, 0.66 mm.
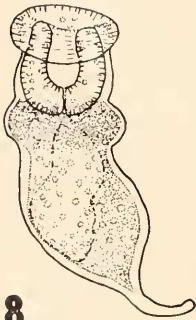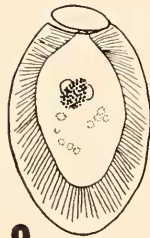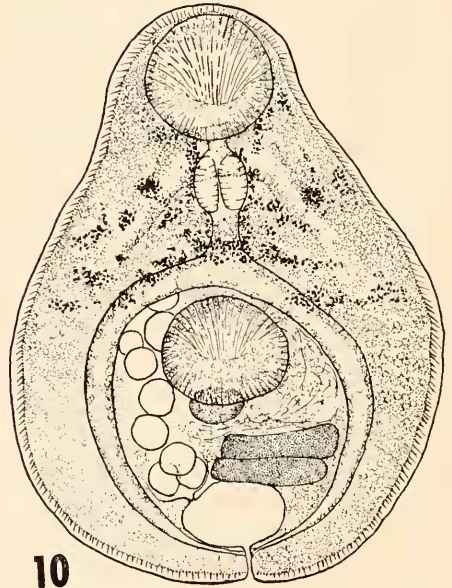
M. leidyi proved to be a favorable intermediate host. *Aurelia aurita* was not susceptible; the cercariae made no attempt to penetrate this species.

The cercariae are produced in rediae and there are at least two generations of rediae. Most of the cercariae emerge from the snail during the night or early morning, although some are shed during the day. When released from the snail, they swim at all levels of the water, darting about rapidly, with the body retracted and the long tail in advance. On emergence, they tend to accumulate on the dark side of the container, but when older, by late afternoon or next morning, they collect on the light side of the bowl. They attach by the tips of their tails, which precede in locomotion, at any part of the jelly-fish or ctenophore, but more often on the aboral surface. After attachment, the cercaria turns and enters the tissue anterior end first, advancing by movements of both tail and body. The contents of the penetration-glands are extruded during penetration and subsequent migration of the larvae. When the body becomes firmly embedded in the jelly, the lashing of the tail frees it from the body and it continues to swim, sometimes for hours. The cercariae may attach to the bottom of the container by the tips of their tails which contain glandular cells. In the medusae, the metacercariae became uniformly distributed throughout the body (Fig. 11), whereas in the ctenophores they accumulated at the bases of the combs, sometimes as many as three or four between two combs. The factors determining the cause and course of migration are quite unknown.

Eggs from worms of natural infection have been embryonated (Fig. 9); the miracidia develop and emerge in 9 to 10 days at laboratory temperatures. They have ocelli with conspicuous lenses, long cilia, and swim rapidly. A specimen of *Anachis avara* exposed to unincubated eggs on July 17, 1968 was dissected on August 2; it contained two sporocysts. They were oval, about the same size, 0.060 by 0.050 mm, and the largest germ-ball was 0.021 by 0.016 mm. Four snails exposed on July 23 to embryonated eggs from which miracidia were emerging, were dissected on September 1. All were infected, with two to six sporocysts in each. The sporocysts were oval to irregular in form, 0.30 by 0.25 mm to 0.60 by 0.35 mm. The smaller ones contained germ-balls of different sizes; the larger ones contained first generation or mother rediae in addition to germ-balls, and in one snail there were rediae in the haemal sinuses as well as rediae in sporocysts. The rediae in the sinuses were 0.12 by 0.052 mm to 0.145 by 0.042 mm, and the pharynx measured 0.030 to 0.036 mm; so these rediae were approximately the same size as daughter-rediae of natural infections, found free in the haemal sinuses of naturally infected snails.

The data from life-history aid in clarification of the systematic position of the species. When the cercariae from *A. avara* proved to be the larvae of *Distomum pyriforme* the taxonomic problem was simplified. Substantial differences preclude

FIGURE 5. Redia of *Neopechona,* flattened under coverglass pressure, cercarial germ-ball emerging at birth pore, length, 0.75 mm.

FIGURE 6. Cercaria, outline from sketches of living specimens.

FIGURE 7. Cercaria, morphology from sketches of living specimens.

FIGURE 8. Daughter redia, fixed and stained specimen, 0.12 mm long.

FIGURE 9. Egg, with miracidium, from pencil sketches of emerging larva.

FIGURE 10. Metacercaria, from *Mnemiopsis leidyi,* experimental infection, fixed under coverglass pressure, ventral view, specimen 0.18 mm long.

the allocation of the species *pyriforme* to the genus *Opechona*, and it is designated as type of a new genus, *Neopechona,* in the subfamily Lepocreadiinae.

<div align="center">NEOPECHONA GEN. NOV.</div>

Diagnosis

Lepocreadiidae, Lepocreadiinae. Distomes with ovate to pyriform body, cuticle armed, cirrus and metraterm spinose. Acetabulum preequatorial. Oral sucker readily inverted, about the same size as the acetabulum, prepharynx and epithelial pseudo-esophagus present, ceca long, unite with terminal portion of the excretory vesicle to form the uroproct. Testes two, contiguous, diagonal to almost tandem, in posterior half of body. Genital pore preacetabular, submedian; cirrus sac clavate, extends almost to level of ovary, contains cirrus, prostatic cells and internal seminal vesicle; external seminal vesicle large. Ovary on right side, pretesticular; Laurer's canal and seminal receptacle present; metraterm short, less than the diameter of the acetabulum. Vitelline follicles from level of pharynx to posterior end of body, dorsal, lateral and ventral to ceca, not confluent in the median plane. Vitelline receptacle median, pretesticular; uterus short, winding, pretesticular; eggs few, large, not embryonated. Excretory vesicle tubular, dorsal, on right side of body, extends to level of pharynx, contains spherical concretions. Parasites in digestive tract of marine fishes. Asexual stages in gastropods; metacercariae unencysted in medusae and ctenophores. Type species: *Neopechona pyriforme* (Linton, 1900) new combination. Synonyms: *Distomum pyriforme* Linton, 1900; *Lepocreadium pyriforme* (Linton, 1940) (in part).

Differential diagnosis

Neopechona shares characters with both *Lepocreadium* and *Opechona*. In the key to genera of Lepocreadiinae Odhner, 1905, formulated by Yamaguti (1958), *Neopechona* is closest to *Opechonoides* Yamaguti, 1940. But it differs from that genus in length of ceca, location of testes, position of vitelline receptacle, and extent of vitelline follicles.

<div align="center">DESCRIPTIONS</div>

Adult

A large, living specimen measured without pressure, in contracted condition was 0.60 mm long and 0.052 mm wide; extended it was 1.80 mm long and 0.25 mm wide. Fixed and stained gravid specimens (Figs. 1, 3, 4) measure 0.32 to 0.82 mm in length and 0.25 to 0.40 mm in width. The largest juvenile specimen (Fig. 2) is 0.36 mm long and 0.16 mm wide. The body is pyriform, widest posteriorly, at the level of the testes. The anterior end is mobile; when extended and narrowed, the prepharynx may be as long as the diameter of the oral sucker and the pseudo-esophagus may be almost as long. However, the anterior end is usually not extended and frequently it is retracted with the oral sucker introverted within the anterior end of the body. In normal condition (Figs. 1, 2, 4), both prepharynx and pseudo-esophagus are evident. In young specimens, diffuse pigment, from the disintegration of the ocelli, may be present in the lateral areas at the level of the

pharynx. The cuticula is spined throughout, the spines are about 0.005 mm long, imbricate, set closely in the anterior part of the body, becoming sparser posteriorly. The musculature of the body-wall is not strongly developed and in gravid specimens, the reproductive structures are so predominant that mobility is restricted. The acetabulum is situated about one-third of the body length from the anterior end; it is 0.07 to 0.09 mm in diameter, the measurement is influenced by the degree of pressure exerted by the coverglass. The oral sucker is approximately the same size. The pharynx is 0.035 to 0.043 mm in diameter; it is almost spherical although it becomes longer in the anteroposterior axis when the anterior portion of the body is extended. The pseudo-esophagus is lined with epithelium, continuous with that of the ceca. The bifurcation of the digestive tract varies in position with extension and retraction of the body, but is situated a short distance anterior to the acetabulum. The ceca extend posteriorly between the vitellaria on the lateral and the gonads on the medial sides, and open into the terminal part of the excretory vesicle, forming the uroproct.

The excretory system was worked out in cercarial and metacercarial stages and persists without change in the adult condition. In adult worms, the concretions may reach 0.014 mm in diameter.
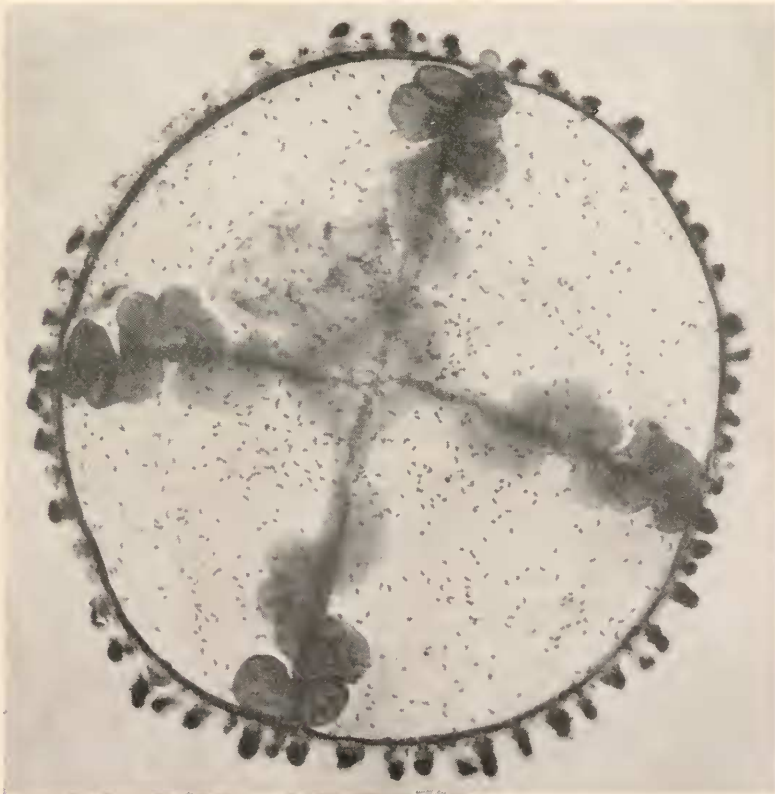

FIGURE 11. Photograph of a specimen of *Gonionemus vertens,* experimental infection of *Neopechona pyriforme,* exposed one day to cercariae; *G. vertens,* 12 mm in diameter.

The testes are situated in the posterior two-fifths of the body, disposed slightly diagonally; typically the posterior testis is slightly larger, and is located on the right side a short distance posterior to the ovary, but their positions are modified by elongation and contraction of the body and by the accumulation of eggs in the uterus. When the body is fully extended, the testes may be almost tandem and when retracted, the organs may be displaced (Fig. 3), in which the anterior testis is shoved toward the right. The testes are notched, but not lobed; they are oval to ovate, longer in the transverse axis, and vary much in size. In mature specimens they measure 0.07 to 0.18 mm in width and 0.04 to 0.09 mm in length. In a large, pressed specimen (Fig. 4), the testes are almost twice as large as in a somewhat smaller specimen (Fig. 1) which was fixed without pressure. In pressed specimens, the worms and their organs appear larger, but the apparent increase in size is the result of flattening. The testes are contiguous and may overlap slightly; sperm ducts arise at the anterior ends and join to form the external seminal vesicle which is continuous with the internal seminal vesicle in the cirrus sac. The external vesicle is usually large, but the size of the vesicles is dependent on the amount of sperm present at any given time. The genital pore is preacetabular, slightly left of the median plane. The cirrus sac is clavate; it extends posteriad in a curved or sinuous course, with the posterior end near the ovary. The internal seminal vesicle is continued by an ejaculatory duct, surrounded by prostatic cells, and the cirrus is eversible. The cirrus and metraterm are spined; the small spines are conspicuous in living specimens, but are not visible in stained and mounted ones.

The ovary is spherical to irregular in shape, 0.04 to 0.07 mm in diameter, sometimes notched, but not lobed, situated on the right side near or slightly posterior to the middle of the body. It is just anterior to the testicular zone and directly ventral to the anterior extension of the excretory vesicle. The oviduct arises at the median, posterior face of the ovary; it passes mediad, receives a duct from the seminal receptacle, gives off Laurer's canal, then receives the common vitelline duct and opens into the ootype, surrounded by the cells of Mehlis' gland. The uterus coils forward between the seminal vesicle and seminal receptacle and posterior part of the cirrus sac, chiefly on the left side of the body; the metraterm is short, about one-half to two-thirds of the diameter of the acetabulum. The vitellaria are extensively developed, extending chiefly in the extracecal fields from the level of the pharynx to the posterior end of the body. Follicles extend dorsal and ventral to the digestive ceca, but are not confluent in the median plane. Longitudinal collecting ducts receive cells from the follicles and, at the postovarian level, ducts from the two sides pass mediad to form the large vitelline receptacle, from which the duct leads to the oviduct. The eggs are thin-shelled, operculate, relatively enormous, 0.056 to 0.062 mm long and 0.036 to 0.040 mm wide, few in number, not embryonated. The operculum is 0.021 mm in diameter. When passed from the worm, the eggs slowly sink in sea water but catch on bits of debris; when embryonated, they are larger, measuring 0.068 to 0.072 mm in length and 0.042 to 0.046 mm in width, contain a bubble of gas and float when loosened. The miracidium (Fig. 9) does not fill the egg-shell; it measures 0.046 by 0.029 mm; the ocellus is 0.007 to 0.008 mm in diameter. The ciliation is uniform except for the apical papilla and the cilia are 0.005 to 0.006 mm in length.

Redia

The haemocoele of a naturally infected snail contains a large number of very small daughter rediae. Figure 8 was made from a specimen that measures 0.13 mm long. In these small rediae, the pharynx is 0.03 to 0.037 mm in diameter, virtually as large as in the large gravid rediae (Fig. 5). The rediae of this species are relatively small, the largest is 0.75 mm long. They are cylindrical, without locomotor appendages, widest near the anterior end, attenuated posteriorly with a curved tail-like tip. The body wall is delicate but in living specimens contraction of the circular muscles may produce one or more constrictions, that may give a redia a collared, neck-like appearance or a dumb-bell shape. The rediae contain orange-yellow pigment and in a few individuals there are pigmented ocelli. The pharynx may be protruded, may be preceded by a ring-like collar, and in many of the fixed and stained specimens, the pharynx is retracted within the anterior portion of the body. The intestine is saccate and very small. The excretory system is double with pores on either side in the posterior portion of the body. From each pore a collecting duct passes anteriad and near the middle of the body it divides into anterior and posterior branches. Each branch has a recurrent tubule and continues toward the corresponding end of the redia where it divides into two tubules. Each tubule terminates in a flame-cell and the excretory pattern (Fig. 5) is identical with that of a very young cercaria. The birth-pore is ventral, near the anterior end (Fig. 5).

Cercaria

The cercariae (Figs. 6, 7) are distomate, ocellate, and trichocercous; they develop in rediae in the haemocoele of the snail, emerge while still immature, and complete their development in the haemal sinuses. The body is oval to pyriform, and may be wider in either the anterior or posterior region. In living specimens, observed under coverglass, the body contracted measured 0.16 mm long and 0.13 mm wide; extended it measured 0.50 mm long and 0.06 mm wide. Under slight coverglass pressure, the bodies of cercariae measure 0.20 to 0.32 mm long and 0.11 to 0.16 mm wide. Fixed in hot whirling fluid, the bodies are 0.15 to 0.19 mm long, 0.085 to 0.095 mm wide and the tails are fully extended, 0.60 to 0.65 mm long. When swimming normally, the body is contracted, almost circular in outline, about 0.12 mm long and the tail is extended, about five times the length of the body. The stem of the tail narrows gradually from base to tip and the median portion is 0.03 to 0.05 mm in width. The tail bears paired setaceous tufts, enclosed in delicate membranes and termed "finlets" by Cable (1954). There are 21 lateral pairs and one terminal pair. The lateral pairs are 0.10 to 0.12 mm long; the terminal ones are 0.073 mm long. The lateral pairs are flattened anteroposteriorly and appear as oars or paddles, which make the tail a powerful swimming organ. Each lateral finlet has a row of five or six rays, rod-like or tubular supports, in dorsoventral alignment. They appear to be formed by a secretion; when the tail disintegrates, the finlets separate from the tail-stem and a widened portion of each ray migrates from the base to the tip where it appears as a minute refractive spherule. Each terminal finlet has only three rays. Under high magnification, the bases of the rays appear multiple, as though three, four, or more strands had fused to form each rod-like support.

On the body, but not the tail of the cercaria, the cuticula contains retrorse spines, arranged in an imbricate pattern. The acetabulum is situated at or near the middle of the body; it is 0.045 to 0.054 mm in diameter, and the opening bears nine papillae (Fig. 7). The ocelli consist of aggregates of irregularly disposed pigment, typically longer in the lateral axis; they are at the level of the pharynx or slightly anterior to it and about the same size as the pharynx.

The oral sucker is spherical to pyriform, often slightly wider in the posterior half; it measures 0.055 to 0.060 mm in diameter. The pharynx is 0.016 to 0.024 mm in diameter; the prepharynx and pseudo-esophagus vary in length as the anterior end of the body is extended and retracted, and either may be as long as the pharynx. The digestive tract bifurcates a short distance anterior to the acetabulum. The pseudo-esophagus is lined with epithelium, continuous with that of the ceca. The ceca extend laterally and caudally, opening into the posterior end of the excretory vesicle.

There are eight pairs of penetration-glands, situated in the lateral areas between the ocelli and the level of the acetabulum. On either side, ducts from three cells pass forward, lateral to the ocellus and dorsal to the excretory tubules, while ducts from the other five cells pass mediad of the ocellus and around and above the oral sucker. All ducts open to the surface at the anterior end of the cercaria, above the opening of the oral sucker. The glands are spherical to oval, about 0.010 mm in diameter, often partially superimposed. They become oval to elongate under pressure as the secretion passes from the body of the cell into the duct. The primordia of the gonads are clearly recognizable, situated in the caudal one-fourth of the body.

The excretory system does not extend into the tail. In the young cercaria it is double, with pores on either side, near the posterior end of the body, and collecting ducts that extend forward and contain tufts of cilia as they turn posteriad. After a short recurrent portion, each collecting duct divides into anterior and posterior branches. Each branch gives off a recurrent tubule and later divides to form two terminal tubules; each tubule terminates in a flame-cell and the formula is $2 [(1 + 1 + 1) + (1 + 1 + 1)]$. Later, a constriction at the level of the excretory pores cuts off the tail and the posterior portions of the collecting ducts fuse in the median plane to form the primordium of the excretory vesicle. At the same time, the posterior ends of the digestive ceca unite with the caudal portion of the excretory vesicle to form the uroproct. From the anterior end of the fused portions of the collecting ducts, a median dorsal extension develops, forming a thin-walled reserve excretory vesicle, which becomes filled with fluid and may extend to the level of the pharynx. This vesicle later contains concretions, usually disposed in a linear series, but sometimes, on retraction of the body, they may be in a zigzag pattern or in a double row. The concretions vary in size from granules or globules to concentric layers of refractive material as much as 0.14 mm in diameter. The portion of the median vesicle immediately anterior to the uroproct forms a pulsatile bladder, separated by sphincters from the uroproct and the more anterior portion of the vesicle. On either side of the pulsatile bladder, a collecting duct, lined with cilia, passes forward, lateral to the digestive cecum. Anterior to the acetabulum the collecting duct divides into anterior and posterior branches. The anterior branch extends almost to the ocellus of that side where it divides to form a duct that passes forward and a duct that turns backward. The

anterior duct passes forward, gives off a recurrent tubule that leads to a flame-cell situated just anterior and lateral to the ocellus, then a tubule to a flame-cell located just posterior to the oral sucker, and divides to supply two flame-cells that are lateral to the oral sucker.   The backward branch gives off a duct that supplies a group of four cells and continues posteriad where it gives rise to a third group of four cells.   In each group, the tubules and flame-cells are disposed in the same manner as described for the most anterior one.   In the posterior half of the body, the backward branch of the collecting duct divides forming a pattern that is just the obverse of that in the anterior half of the body.   The flame-cell formula of the mature cercaria is $2 [(4 + 4 + 4) + (4 + 4 + 4)]$, with six groups of four cells on each side of the body.   The most anterior group supplies the preocellar area; the second group the postocellar area; the third group the acetabular area; the fourth group the postacetabular, pretesticular area; the fifth group the testicular area; and the last group supplies the posttesticular region.

Metacercaria

The metacercariae (Figs. 10, 11) are unencysted and mobile; they are only slightly larger than the cercariae.   The pigment of the ocelli becomes dispersed, but otherwise there is little change from the cercarial condition.

Discussion

The discovery of the life-history of *N. pyriforme* and its systematic relations adds another link in the chain of evidence that integrates life-cycles, larval stages, developmental features and adult morphology with taxonomy of the digenetic trematodes.   The group of trichocercous cercariae was proposed by Lühe (1909) for those species which have the "Schwanz mit Borsten besetz (marin)."   These larvae have long been known; *Cercaria setifera* was described by O. F. Müller (1786) but there is no assurance that it is identical with *Cercaria setifera* Joh. Müller (1850).   This species, described by Müller, was named by Moulinie (1856). However, it is certain that *Cercaria setifera* of Monticelli (1888, 1914) is not conspecific with that of Müller, 1850.   The first suggestion concerning the life-history of the trichocercous cercariae was made by Odhner (1914) who, on the basis of morphological agreement, asserted that *C. setifera* of Monticelli is the larva of *Lepocreadium album* (Stossich, 1890) Stossich, 1904.   Dollfus (1925) noted that *C. setifera* of Monticelli is distinct from *C. setifera* Müller, 1850; he gave a summary of the trichocercous larvae known at that time and divided the marine species into two groups, one in which ocelli are present and one in which they are absent.   Commenting on this arrangement, Cable (1954) observed, p. 18, "subsequent studies have revealed that such a distinction may be an artificial one, for instances are known in which one cercaria may be ocellate whereas another larva in the same family lacks eye-spots.   On the basis of known life histories, it is certain that the trichocercous cercariae listed by Dollfus have adults belonging to three distinct families, the Lepocreadiidae, the Monorchiidae, and the Fello-distomatidae.   Furthermore, the last two groups and perhaps all three have some larvae that are not trichocercous.   Thus in distinguishing the larvae of these families, the morphology of the body and type of molluscan host are more dependable than is the structure of the tail which can be positively misleading.

Of the non-ocellate cercariae listed by Dollfus, *C. setifera* Müller *nec* Monticelli (the larva of *Bacciger bacciger* according to Palombi (1934a), *C. villoti, C. pelsenecri, C. chiltoni,* and *C. pectinata* Huet *nec* Chilton may be assigned to the Fellodistomatidae." Dollfus recognized disparity among trichocercous cercariae; he (1927) reported an unnamed setigerous larva taken in plankton near Cherbourg, France, stated that it is not identical with *C. setifera* of the Mediterranean, and expressed the opinion that not all trichocercous cercariae are members of *Lepocreadium.* Indeed, Lebour (1917) had described and figured a trichocercous cercaria found in plankton at Plymouth, England, as identical with the unencysted metacercariae in medusae and ctenophores which she (1916) had recognized as larvae of *Pharyngora bacillaris* (Molin, 1859), a common parasite of *Scomber scombrus* and *Gadus merlangus.* Palombi (1934a) announced that *C. setifera* Müller, 1850 develops in sporocysts in *Tapes decussatus;* that the metacercariae occur in the amphipod, *Erichtonius difformis,* and that the adult is *Bacciger bacciger* (Rudolphi, 1819) Nicoll, 1914, a parasite in various members of the genus *Atherina.* As synonyms of *B. bacciger,* Yamaguti (1958) listed *Cerceria lata* Lespès, 1857; *C. lutea* Giard, 1897; and *C. pectinata* Huet, 1891. Palombi (1934b, 1937) reported that *C. setifera* Monticelli, 1914 (in part) *nec* Müller, 1850, is the larva of *Lepocreadium album* (Stossich, 1890). The cercariae are produced in rediae in *Nassa mutabilis,* encyst in *Aplysia punctata* and *Tapes* spp., and become adult in various species of fish. This species was studied by Arvy (1953) who declared, p. 298, "Vue à des stades divers, sur des hôtes variés, dont je me suis appliquée à relever la liste, *Cercaria setifera* Monticelli a reçu des noms divers, mais il semble bien que, dans tous les cas auxquels j'ai fait allusion, il s'agisse de la même larve d'Allocreadiidae." Martin (1938) showed that *Cercaria setiferoides* Miller and Northup, 1926, produced in rediae in *Nassarius obsoletus* of the Woods Hole, Massachusetts area, is the larval stage of a species of *Lepocreadium.* He reported penetration and encystment in the turbellarian, *Procerodes warreni,* and in spionid annelids, although he predicated that these experimental hosts may not be the natural ones. The discovery of the life-cycle and larval stages of *Lepocreadium pegorchis* (Stossich, 1890) by Bartoli (1967) demonstrates the variation in cercarial morphology that may occur in species of a single genus. The cercariae are produced in rediae in *Nassa mutabilis,* but differ distinctly from those of *L. album* (Stossich, 1890), found in the same host, and from *L. setiferoides* (Miller and Northup, 1926) which develop in *Nassarius obsoletus* in America. In *L. pegorchis,* the tail of the cercaria is much shorter than the body, is only weakly functional, and the larvae seldom leave the substratum. They are drawn in the inhalant siphons of various lamellibranch mollusks, where they penetrate the tissues but do not encyst.

A comprehensive account of marine cercariae was given by Holliman (1961) who attempted to assign them to systematic categories. Dollfus (1963) listed the Palearctic and Indian marine coelenterates which harbor larvae of digenetic trematodes. The hosts are mainly planktonic and manifest little specificity. He noted that cercariae of the Lepocreadioidea are produced in rediae, have ocelli, and do not encyst. Accordingly, since Palombi (1937) reported encystment of metacercariae of *L. album,* Dollfus suggested that he may have been dealing with more than one species. Consideration of the life-cycles of digenetic trematodes with correlation of intermediate and final hosts, of larval stages, cercarial types,

and systematic relations, discloses one of the enigmas of theoretical zoology. Commenting on the situation, Stunkard (1967b) predicated, p. 675, "The course of development reflects, to a considerable extent, the evolutionary history of the species. In endoparasitic animals, the individual perishes with the host and larval stages provide for dispersal and perpetuation of the species. The origin and significance of larval stages find their explanation in the life-cycles of the species in which they occur. According to Leuckart (1891a) larval structures are adaptations for earlier independent existence of offspring with consequent increase in reproductive capacity. Larval adaptations may be as complete and perfect as those of adult individuals." Stunkard reasoned that the digenetic trematodes were derived from turbellarian-like ancestors, that they became parasites of mollusks in Cambrian time, and that with the advent of fishes and their ingestion of mollusks, the sexual stages of the worms were deferred to the definitive hosts while former hosts were relegated to an intermediate status. Mollusks still serve as first hosts and harbor the initial stages in the life-cycle.

Summary

The digenetic trematode described by Linton (1900) as *Distoma pyriforme* has been reported from many hosts and several species have been included in the accounts, with resultant confusion. It was included in the genus *Lepocreadium* Stossich, 1904 by Linton (1940), but it is not congeneric with *L. album* (Stossich, 1890), type of the genus. Its life-cycle has been elucidated; *Anachis avara* is the first intermediate host, where cercariae are produced in rediae. The cercariae are ophthalmotrichocercous, swim actively with the tail in advance. They penetrate but do not encyst in certain hydrozoan and scyphozoan medusae and in the ctenophore, *Mnemiopsis leidyi*. Developmental and adult stages resulted from ingestion of metaceracariae by the scup, *Stenotomus chrysops*. Eggs from worms were embryonated; miracidia emerged in 8 to 10 days, penetrated into *A. avara*, transformed into sporocysts, and produced rediae in 5–6 weeks. Worms recovered from *S. chrysops* are assigned to a new genus, *Neopechona*, and redescribed as *N. pyriforme* (Linton, 1900) new combination. The genus is included in the subfamily Lepocreadiinae Odhner, 1905.

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